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Caesalpinioideae and the study of forest refuges in Gabon : Preliminary results

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Summary : The present study shows that modern distribution data of Caesalpinioidous taxa can be used in the study on forest refuges. Preliminary results indicate that previously proposed locations of forest refuges in central Africa are not correctly situated and that a distinction should be made between lowland and montane forest refuges. The geographic position of postulated forest refuges in Gabon needs to be reviewed with regard to new distribution data. Further, more detailed research on the biogeographic history of these areas during the last glacial is necessary, preferably involving a combination of (paleo)biological and (paleo)climatological studies, to test the new suppositions.

Résumé : Cette étude montre que les données fournies par la distribution actuelle des taxons de *Caesalpinioideae* peuvent être utilisées pour étudier les refuges forestiers. Des résultats préliminaires indiquent que les emplacements supposés des refuges forestiers n'ont pas été correctement situés et qu'une distinction doit être faite entre refuges forestiers de plaine et de montagne. La position géographique supposée des refuges forestiers au Gabon doit être revue à la lumière des données récentes de distribution. En outre, d'autres recherches approfondies, relatives à l'histoire biogéographique de ces territoires au cours de la dernière glaciation, sont nécessaires, incluant de préférence une combinaison d'études (paléo)biologiques et (paléo)climatologiques, pour tester les nouvelles hypothèses.

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INTRODUCTION

During the last glacial (approximately 75,000-12,000 years B.P.) climatic conditions were quite different from those prevailing in equatorial Africa today. The average temperature was 3-6°C lower, the annual amount of precipitation was considerably less and the dry season lasted longer ; with the extent of the deviation of these variables depending on location and time (Livingstone, 1982 ; Maley, 1987 ; Maley, 1989). Consequently, during this period, the vast expanse of tropical rain forest had been reduced to a few, relatively small and isolated patches (tropical forest refuges).

Evidence for the geographic position of these tropical rain forest refuges can be deduced from data on biotic diversity combined with biogeographic, geological and (palaeo)palynological information.

MALEY (1987) published a map (see Fig. 1) representing postulated tropical lowland rain forest refuges in equatorial Africa.

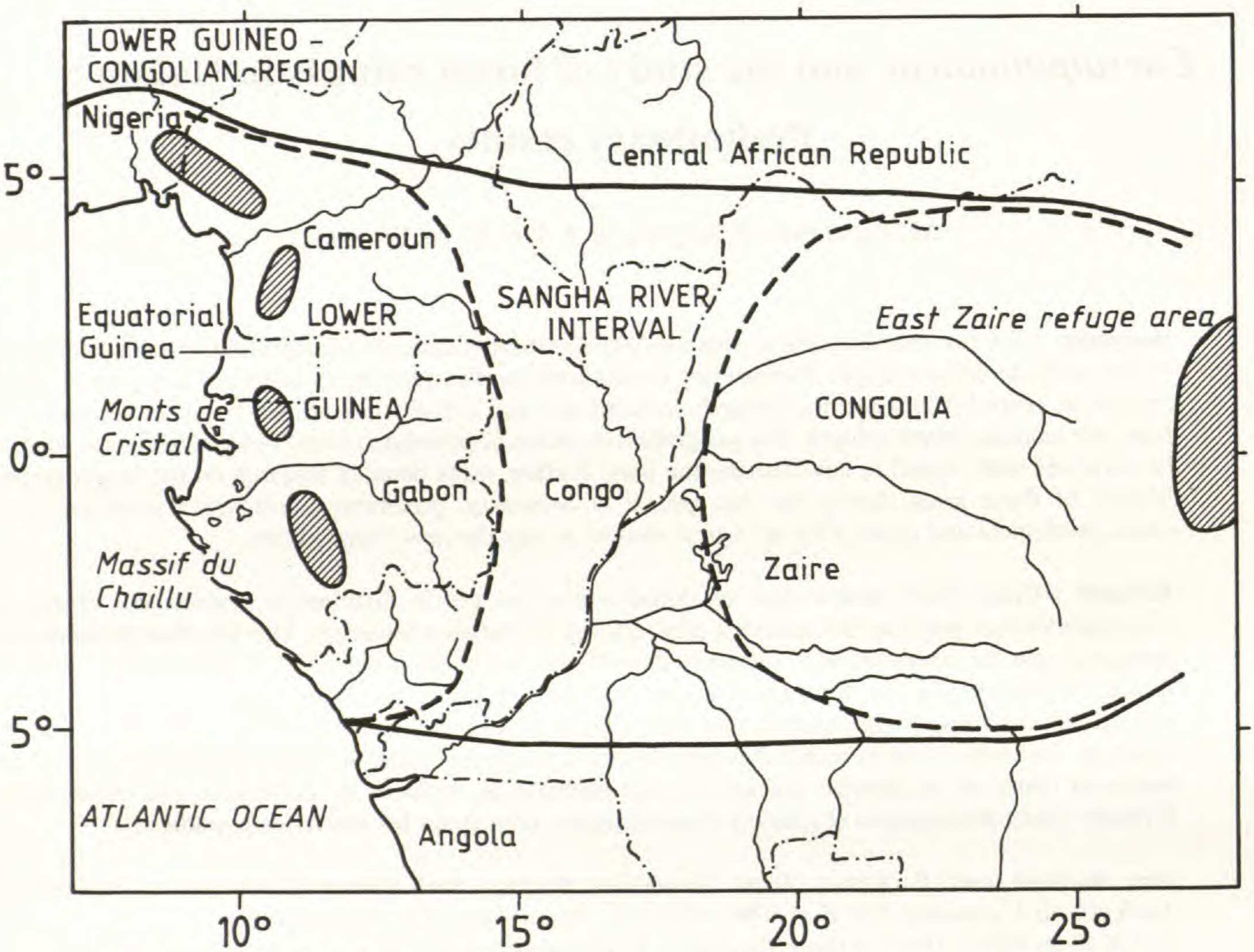

Fig. 1. — Location of the main lowland rain forest refuges in equatorial Africa, ca. 18,000 yr B.P. according to MALEY (1987, 1989) and phytochoria of the Lower Guineo-Congolian Region according to WHITE (1979).

To delimitate the forest refuges in Gabon, MALEY used data on modern biotic diversity and gradients of declining numbers of species (such as published a.o. by HAMILTON, 1982), combined with data on local orographic climatic effects. Two rain forest refuges are postulated in relatively elevated areas in Gabon (Monts de Cristal in the north and Massif du Chaillu in the south : max. altitude ca. 1000 m) as well as another two in south-west Cameroon and a much larger one in eastern Zaire.

However, new evidence leading to a more precise location and specification in vegetation zones of these areas in Gabon is becoming available (SOSEF, 1992 ; REITSMA et al., 1992). SOSEF (1992) poin-

ted out that a clear distinction should be made between lowland and montane rain forest refuges. It was shown that *montane* forest once occurred in the Massif du Chaillu (MALEY et al., 1990). Additionally, in a study on the vegetation of inselbergs and rocky outcrops in Gabon, REITSMA et al. (1992) shed doubt on the correct location of the forest refuge in the Monts de Cristal as postulated by MALEY. According to them, this area should be situated at lower altitudes and located more to the west.

Gabon's present lowland rain forest covers approximately 80 % of the country. Supposing that this forest was restricted to small and isolated patches during the last glacial, it is most likely that the subsequent later expansion and present day distribution of this forest type found its origin in these areas. The increase of the average temperature and annual amount of precipitation and the decrease of the length of the dry season from 12,000 B.P. onward, made this expansion possible. At present the annual rainfall ranges from 3,600 mm in the north-west near the border with Equatorial Guinea to less than 1,600 mm in the north-east and the south-west. There is a distinct dry season of 3–4 months.

The purpose of this study is to show that the distribution patterns displayed by a selection of Gabonese *Caesalpinioideae* species can be used in determinating the position of forest refuges in central Africa as postulated by MALEY, with emphasis on Gabon. For details about this pilot study the reader is referred to RIETKERK (1993).

MATERIAL AND METHODS

Caesalpinioideae play a dominant role in the ecology of lowland rain forests in equatorial Africa (LETOUZEY, 1985 ; HLADIK, 1986 ; REITSMA, 1988 ; BRETELER, 1990). The dispersability of at least a part of its species is estimated to be extremely low (EVRARD, 1968 ; WHITE, 1983 ; WILKS, 1990 ; BINGHAM, 1991). Assuming that some species " captured " in refuges during the last glacial were not capable of migrating out of these areas rapidly when conditions again improved, while others dispersed more quickly to new areas, the present distribution of these *Caesalpinioideae* could provide additional data for delineating the location of evergreen lowland forest refuges in central Africa. The hypothesis at the root of this idea is that the distributions should show centres of frequency of occurrence, as well as concentrations of species, corresponding to areas from which the species migrated.

A selection of 28 taxa from the 158 species cited in the *Flore du Gabon* (AUBRÉVILLE, 1968) was made. This selection includes species with different fruit and seed characteristics and is based on the underlying hypothesis that these differences could consequently lead to different dispersal capacities and ultimately to different distribution patterns. The selected species are listed in Table 1.

For each species a spot distribution map was made for central Africa, compiled from specimens present in Herbarium Vadense (WAG), Jardin Botanique National de Belgique (BR) and Muséum National d'Histoire Naturelle, Paris (P). The identification of the specimens is based on determinations, most often by specialists, annotated on the collections.

The distributions of the species were then analyzed in a search for groups of species (biogeographical elements) showing discrete patterns. Such groups were indeed recognized.

In order to characterize these species groups and their patterns, they were compared with categorized groups of species and recognized biogeographical units within the forest flora of western tropical

Africa (WHITE, 1979, see Fig. 1). WHITE 's (1979) analysis of the distributions of 337 species included trees, shrubs and lianas belonging to 12 families.

The next step was to compare the patterns found in the distributions of the studied *Caesalpinioideae* species with the position of the postulated refuges in the region, particularly in Gabon.

TABLE 1 : The selection of 28 species in *Caesalpinioideae*.

Afzelia bipindensis Harms
Afzelia pachyloba Harms
Aphanocalyx cynometroides Oliv.
Berlinia bracteosa Benth.
Berlinia confusa Hoyle
Brachystegia zenkeri Harms / *B. laurentii* (De Wild.) Louis ex Hoyle, species complex
Cynometra mannii Oliv.
Detarium macrocarpum Harms
Didelotia letouzeyi Pellegr.
Eurypetalum tessmannii Harms / *E. batesii* Baker f., species complex
Eurypetalum unijugum Harms
Gossweilerodendron balsamiferum (Vermoesen) Harms
Guibourtia arnoldiana (De Wild. & Dur.) J. Léonard
Guibourtia tessmannii Harms
Hylodendron gabunense Taub.
Hymenostegia klainei Pierre ex. Pellegr.
Monopetalanthus durandii F. Hallé & Normand
Monopetalanthus heitzii Pellegr.
Neochevalierodendron stephanii (A. Chev.) J. Léonard
Oddoniodendron micranthum (Harms) Baker f.
Oxystigma buchholzii Harms
Oxystigma mannii (Baill.) Harms
Pachyelasma tessmannii (Harms) Harms
Pterygopodium oxyphyllum Harms
Scorodophloeus zenkeri Harms
Sindora klaineana Pierre ex. Pellegr.
Tessmannia africana Harms
Tetraberlinia moreliana Aubr.

RESULTS

PRESENT DISTRIBUTION IN RELATION TO THE BIOGEOGRAPHICAL UNITS RECOGNIZED BY WHITE.

An analysis of the distributions leads to the recognition of four groups of species, each group with a discrete distribution pattern. These patterns were found to be concordant with biogeographical units

previously discerned by WHITE (1979). As a consequence, WHITE's denomination was used to characterize our species groups. The classification of the studied *Caesalpinioideae* species according to their distributions in four groups (biogeographical elements) is presented (Table 2).

TABLE 2 : Classification of 28 *Caesalpinioideae* species into biogeographical elements, based on their distributions. See text for further explanation.

Endemics
Berlinia confusa
Cynometra mannii
Didelotia letouzeyi
Eurypetalum tessmannii s.l.
Eurypetalum unijugum
Guibourtia arnoldiana
Guibourtia tessmannii
Hymenostegia klainei
Monopetalanthus durandii
Monopetalanthus heitzii
Neochevalierodendron stephanii
Sindora klaineana
Tetraberlinia moreliana

Marginal intruders
Afzelia pachyloba
Berlinia bracteosa
Detarium macrocarpum
Hylodendron gabunense
Oddoniodendron micranthum

Linking species
Afzelia bipindensis
Oxystigma buchholzii
Pachyelasma tessmannii
Pterygopodium oxyphyllum
Scorodophloeus zenkeri
Tessmannia africana

Disjunct linking species
Aphanocalyx cynometroides
Brachystegia zenkeri s.l.
Gossweilerodendron balsamiferum
Oxystigma mannii

I. **Endemics** : Species with a distribution restricted to Lower Guinea. This group includes 13 (46 %) of the 28 selected species. The distributions of 6 species from this group are presented in Fig. 2.

II. **Marginal intruders** : Species which are characteristic of Lower Guinea, but are also sparingly present in adjacent phytochoria. Five of the studied species (18 %) belong to this group. The distributions of 2 of them are presented in Fig. 3.

III. **Linking species** : Species which occur in the whole Lower Guineo-Congolian Region, although with limited representation in the Sangha River Interval. This group includes 6 (21 %) of the species. The distribution of 3 species from this group is presented in Fig. 4.

IV. **Disjunct linking species** : These species have a distribution similar to that of the linking species, but they are not occuring in the Sangha River Interval. This group includes 4 (14 %) of the species. The distribution of 3 species from this group is presented in Fig. 5.

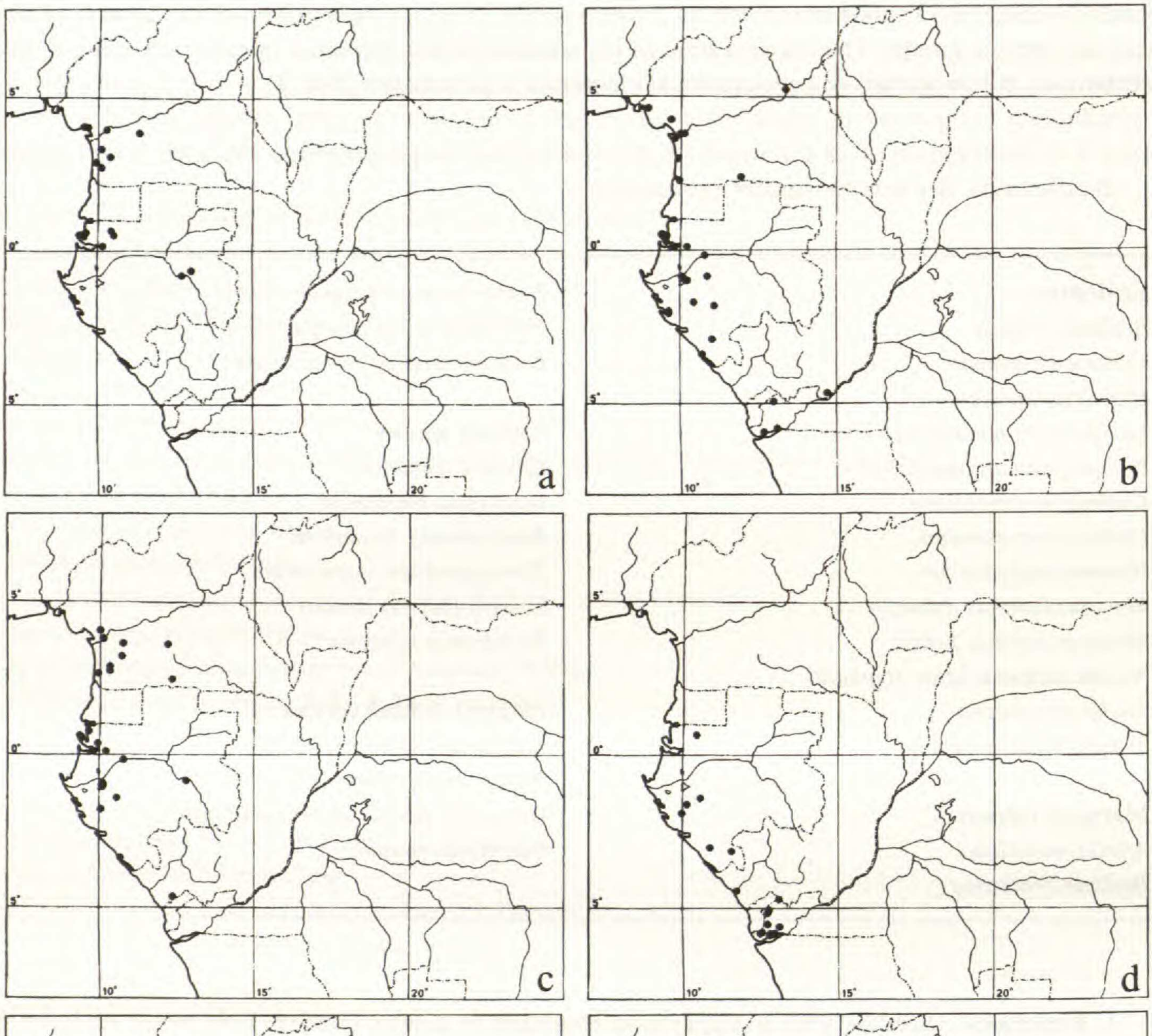

Fig. 2. — Distribution of **Berlinia confusa (a)**, **Cynometra mannii (b)**, **Didelotia letouzeyi (c)**, **Guibourtia arnoldiana (d)**, **Monopetalanthus heitzii (e)**, and **Tetraberlinia moreliania (f)**, in central Africa, examples of endemic species.

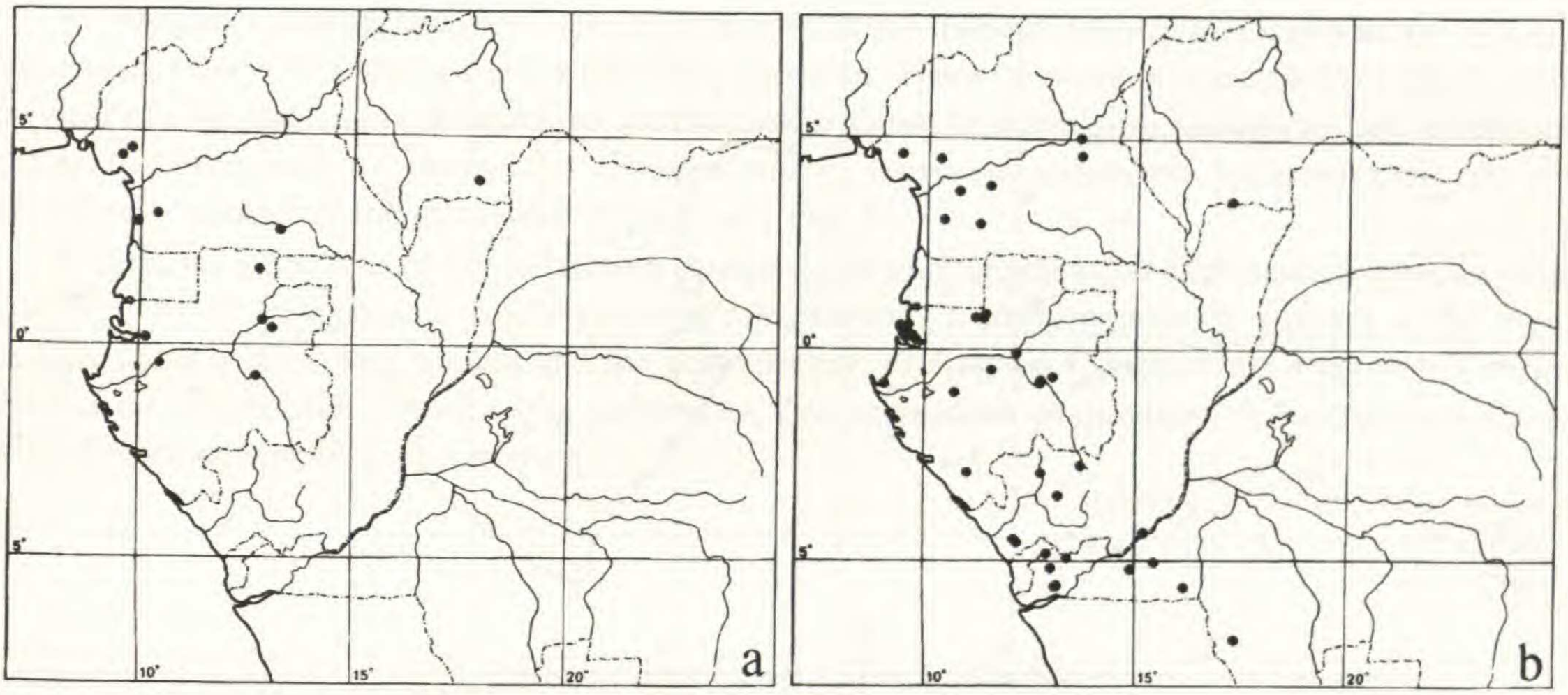

Fig. 3. — Distribution of **Detarium macrocarpum** (**a**), and **Hylodendron gabunense** (**b**), in central Africa, examples of marginal intruders.

The maps in the present study may be considered as good examples of the four discrete distribution patterns. For the spot distribution maps of all 28 *Caesalpinioideae* species, the reader is referred to RIETKERK (1993).

PRESENT DISTRIBUTION IN RELATION TO POSTULATED REFUGES IN THE AREA.

In comparing the present distribution patterns of the species studied with the forest refuges as postulated by MALEY, the following observations can be made.

I. **Endemics** : The endemics all have a limited distribution and show centres of frequency and concentrations of species in Gabon and/or Cameroon. These centres however do not coincide with the postulated refuges, but are located in areas mainly bordering the refuges to the west and along the Ogooué river. Good examples are *Berlinia confusa* with two centres, one in north-west Gabon and one in Cameroon, and *Monopetalanthus heitzii* and *Tetraberlinia moreliana* with two centres of frequency in Gabon (see Fig. 2).

II. **Marginal intruders** : The marginal intruders have a wider range of distribution with less clear centres. Eventual centres all seem to occur in the periphery of the postulated refuges, east as well as west of them. *Detarium macrocarpum* and *Hylodendron gabunense* (see Fig. 3) are good examples.

III. **Linking species** : These more widely ranging species not only show centres of frequency in Lower Guinea, but also in Congolia. The centres in Lower Guinea occur also in the periphery (east and west) of the postulated refuges. Good examples are *Pterygopodium oxyphyllum, Scorodophloeus zenkeri* and *Tessmannia africana* (see Fig. 4). The centres in Congolia are less marked, but seem all to be located mainly west of the East Zaire refuge area.

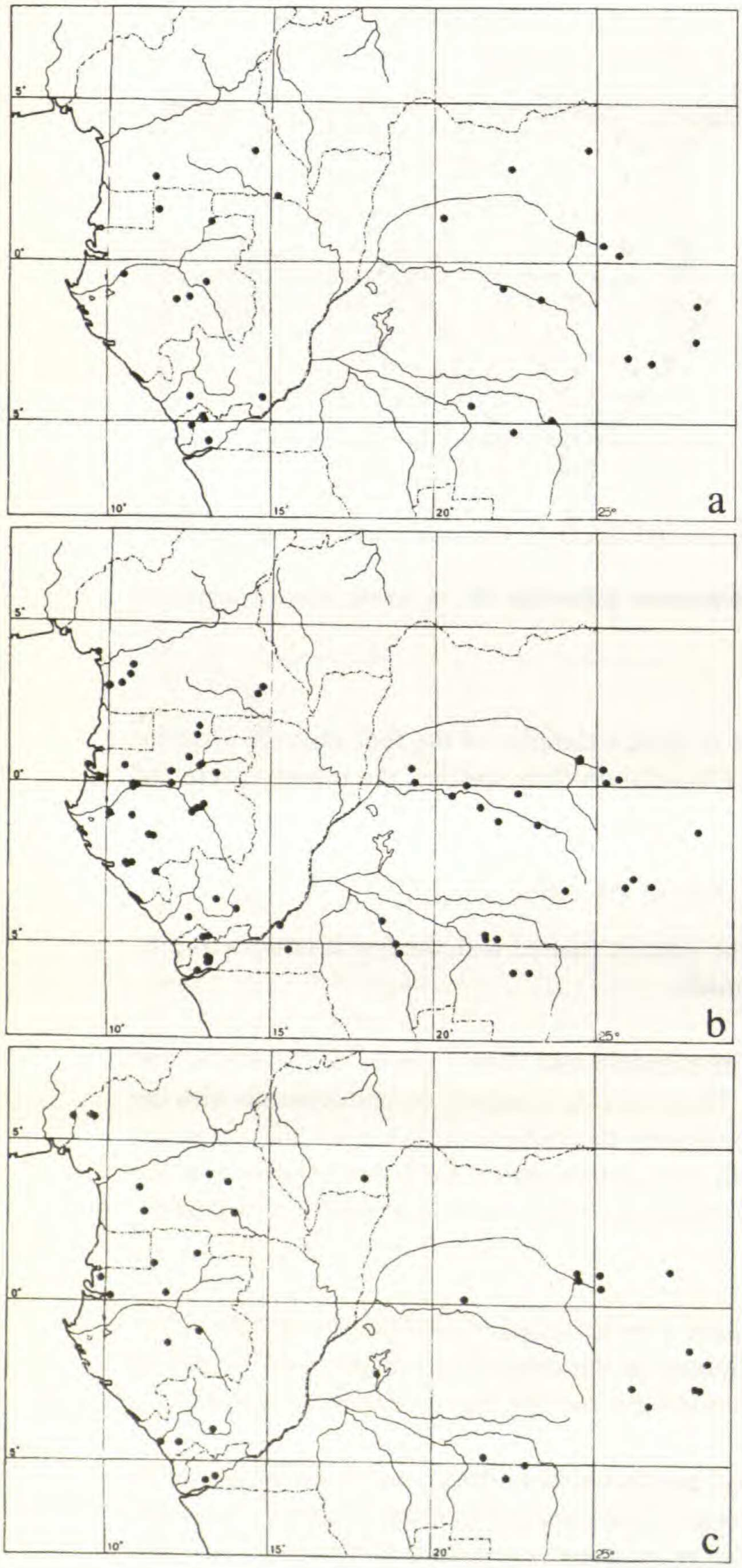

Fig. 4. — Distribution of **Pterygopodium oxyphyllum (a)**, **Scorodophloeus zenkeri (b)**, and **Tessmannia africana (c)**, in central Africa, examples of linking species.

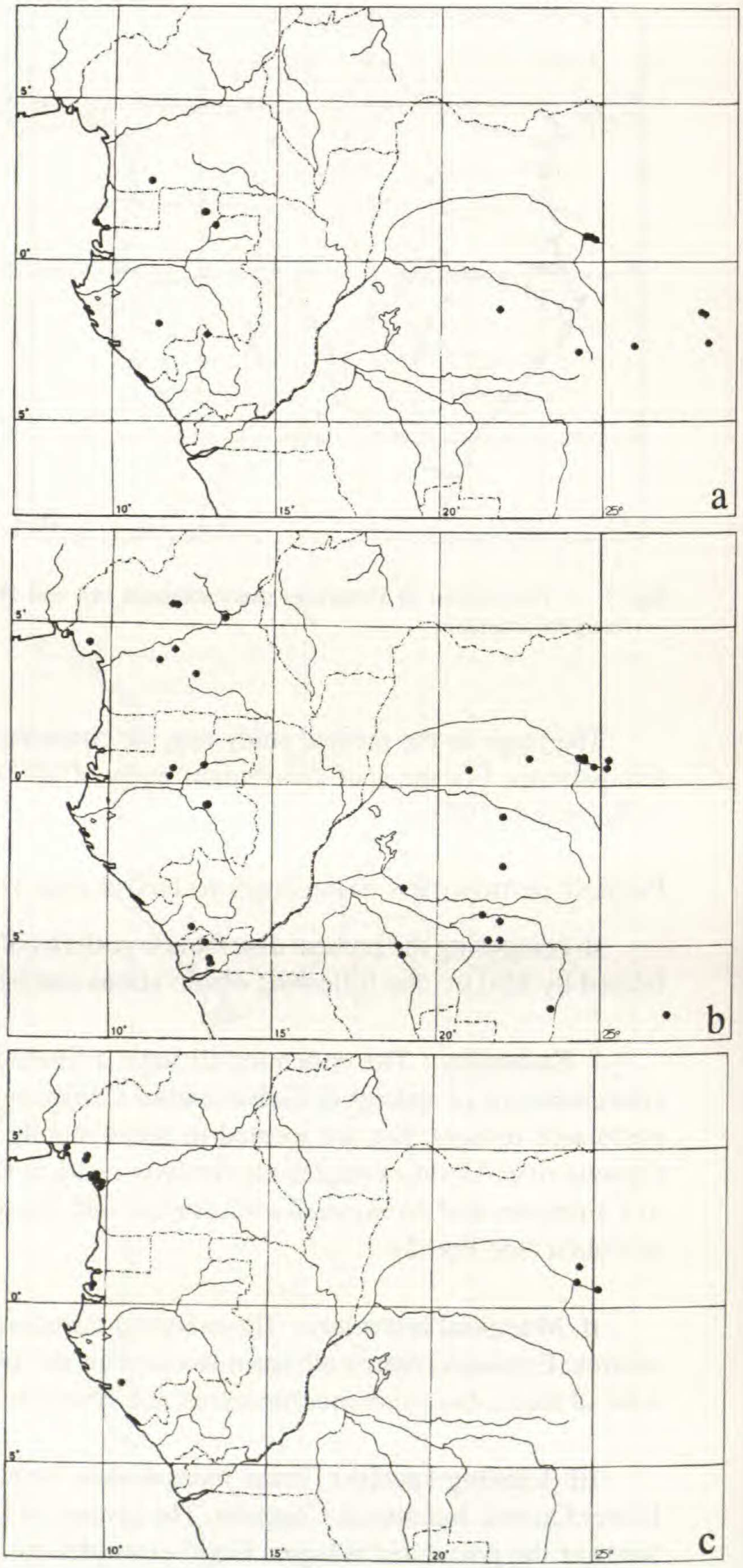

Fig. 5. — Distribution of **Aphanocalyx cynometroides (a)**, **Gossweilerodendron balsamiferum (b)**, and **Oxystigma mannii (c)**, in central Africa, examples of disjunct linking species.

IV. **Disjunct linking species** : The distributions of the disjunct linking species show far less marked centres from which the species might have migrated. There seems to be a centre in Congolia, close to (west of) the East Zaire refuge area. In the Lower Guinean subregion, the species are mainly restricted to areas east (*Aphanocalyx cynometroides, Gossweilerodendron balsamiferum*) or west (*Oxystigma mannii*) of the postulated refuges (see Fig. 5).

Considering the distribution of all four groups together, it appears that each contains species which have a centre of frequency in south-western Zaire (forming a concentration of species), in the region roughly located between Cabinda and the northern part of Angola. Examples are *Cynometra mannii, Guibourtia arnoldiana, Hylodendron gabunense, Pterygopodium oxyphyllum, Scorodophloeus zenkeri, Gossweilerodendron balsamiferum.*

DISCUSSION AND CONCLUSIONS

The analysis of the distributions of 28 species of *Caesalpinioideae* reveals that the centres of frequency and concentrations of species are not in line with the location and delimitation of rain forest refuge areas in Gabon as proposed by MALEY (1987). The patterns found indicate that these areas might have been considerably larger. While lowland rain forest survived in the peripheral lower parts of the refuges, mountain forest covered the central higher parts at ca. 700-1000 m altitude. The observed patterns in relation to the Gabonese refuge areas support the opinion of SOSEF (1992) that true lowland rain forest species could only have survived in a comparatively narrow altitudinal zone between sealevel and 300 m. Between approximately 300 m and 700 m a transition zone from lowland towards mountain rain forest was present, comparable to similar modern transitions as described and summarized by WHITE (1983).

The present centres of frequency and concentrations of the endemic *Caesalpinioideae* species appear mainly in areas south-west adjacent to the postulated refuges. Here we come to the same conclusion as REITSMA et al. (1992) who postulate that the proposed refuge area of the lowland tropical evergreen forest on the Monts de Cristal should be located at lower altitudes and more to the west. However, we suggest that the eastern peripheral part of the postulated refuge area should also be considered as refuge of the lowland tropical evergreen forest. Further research to test this hypothesis is necessary.

The linking and the disjunct linking species all seem to have at least one centre of frequency in the eastern part of their range, not coinciding with, but slightly westwards of the proposed East Zaire refuge area.

Based on the present distributions of *Cynometra mannii, Guibourtia arnoldiana, Hylodendron gabunense, Pterygopodium oxyphyllum, Scorodophloeus zenkeri, Gossweilerodendron balsamiferum*, and to a lesser extend of *Tessmannia africana*, as well as their observed geographic and topographic relation to the postulated refuge areas in the Lower Guineo-Congolian region (including the East Zaire refuge area), the existence of a new lowland forest refugium is postulated. This refugium is located in the Mayombe Region, in Zaire between Cabinda and the northern part of Angola. In this region we find centres of frequency and concentrations of these species. A similar conclusion was reached by SOSEF (1994) based on his research on *Begonia* species.

It would be presumptious at this stage to present a map with adjustments to the map of MALEY, as such modifications in location and floristic specification would lack sound evidence based on palynological data and ecological data of the species concerned.

The present study clearly shows that patterns found in the modern distribution of forest organisms may contribute to an improved understanding of the history of forest communities (and as such of forest refuge areas). In order to interpretate these patterns in any detail, however, more knowledge about the ecological requirements (ecological amplitudes) of the individual species is needed, as well as information about their dispersal capacity and rates. Such knowledge is presently almost absent even for the major components (large *Caesalpinioidous* tree species) of these forests. A preliminary analysis of possible dispersal mechanisms in relation to distribution patterns did not reveal a clear connection between these phenomena (RIETKERK, 1993). Special attention should be paid to the altitudinal amplitudes of the species. Species which are currently restricted to low altitudes will probably have survived only in refuges found at low levels. Others with a broad altitudinal amplitude might have been able to do so also at higher elevations.

In conclusion, it is argued here that the previously proposed locations of postulated glacial refuges of lowland rain forest in Gabon seem to be untenable. The proposed new locations are situated more to the west and in the peripheral lower parts of the hitherto postulated refuges. The glacial and biogeographic history of these areas has to be worked out in more detail, preferably involving (paleo)biological and (paleo)climatological studies. This is directly relevant for devising strategies for conservation of forest organisms, including their genetic resources, in an environment with increasing negative human impact on the presence and survival of tropical rain forest.

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